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Does behavioral flexibility and tolerance to disturbance explain why eastern grey squirrels and eastern fox squirrels have succeeded in invading urban areas?

By: Brittany Balbag

Introduction

Native biodiversity declines when cities expand because natural habitats are lost and fragmented (Marzluff 2001). Urbanization often leads to biotic homogenization- the replacement of native species by a few, usually exotic, species (Blair 2001). A possible explanation for this shift in dominance is that some species are able to readily adapt or are preadapted to urban environments (Blair 1996). The characteristics of species that are able to dominate urban areas are relatively poorly known (Diamond 1986). Early studies have suggested many specific characteristics that allow a species to persist in a urban landscape such as human commensalism, nesting in holes and trees, and a generalist diet (Møller 2009). Only a few recent studies have tried to identify these traits by comparing traits between urban and rural species (Møller 2009, Kark et. al 2007).

Møller (2009) discovered that urban bird species behave differently than rural species. He found that urban species have a higher degree of behavioral flexibility than rural species as indicated by their higher feeding innovation rates. In birds, behavioral flexibility has been correlated with a species ability to invade or colonize a novel environment (Timmermans and Lefebvre 2001). A certain degree of behavioral flexibility would be required in order for a species to start to explore and exploit novel resources that it would encounter in an urban environment. Møller found that urban species had shorter flight initiation distances (the distance at which a human can approach an animal before it flees) than rural species, which suggests that they are less sensitive to disturbance. Furthermore, he found that urban species in rural

environments have shorter flight initiation distances than rural species which suggests that these species were preadapted to cope with human disturbance. A species success in colonizing an urban environment would depend on its ability to withstand human stressors.

To the best of my knowledge, comparisons among rural and urban species have only been studied in birds. In order to make generalizations about what traits allow a species to colonize an urban environment, other comparisons must be made in other taxonomic groups. Like birds, urbanization has led to biotic homogenization in squirrels. The endangered western grey squirrel (*Sciurus griesus*), douglas squirrel (*Tamiasciurus douglasii*), and red squirrel (*Tamiasciurus hudsonicus*) mainly occur in wooded areas in Washington (Linders and Stinson 2007). Urban areas, on the other hand, are dominated by two introduced squirrel species, the eastern grey squirrel (*Sciurus carolinesis*) and eastern fox squirrel (*Sciurus niger*), both of which are native to the eastern United States (Linders and Stinson 2007). The eastern grey squirrel has the widest range and distribution of all tree squirrel species. It is found across the United States, on the eastern coast of Canada, and in several parts of Europe (Linders and Stinson 2007). The eastern fox squirrel has been introduced to Canada and the western United States (Linders and Stinson 2007).

Eastern grey squirrels and fox squirrels demonstrate a considerable degree of behavioral flexibility. Eastern fox squirrels have been observed to utilize novel objects such as cables as a means of traveling throughout their home range and demonstrate flexibility in their use of different orientation cues (King 2004, Waisman and Jacobs 2008). Eastern fox squirrels and grey squirrels demonstrate considerable plasticity in their preference for nest-tree species available and are willing to nest in residential areas in Los Angeles (King 2004, Mosby 1969). In contrast, native western grey squirrels nest only in oak and eucalyptus trees and are unwilling to nest in

residential areas (King 2004). Fisher and Merriam (2000) found that eastern grey squirrels are flexible in their preference for habitat, relying on both agricultural and wooded habitats. In addition, eastern grey squirrels demonstrate their degree of behavioral flexibility by their ability to memorize where other squirrel species have stored their nuts (Wauters et. al 2002). Furthermore, social flexibility has been suggested as one reason why eastern grey and fox squirrels are able to persist in fragmented urban landscapes (Koprowski 2005). Population densities are noted to be higher in fragmented landscapes (Fisher and Merriam 2000). Eastern grey squirrels and fox squirrels accommodate to changes in population density by reducing home range sizes (Don 1983, Baumgartner 1943). Also in highly dense populations, female eastern grey squirrels form kin groups (Koprowski 1996).

The objective of the proposed study is to determine if behavioral flexibility and tolerance to disturbance explain why eastern grey squirrels and fox squirrels have succeeded in invading urban areas. In order to do this, I plan to compare eastern grey squirrels and fox squirrel's behavioral flexibility and sensitivity to human disturbance to two rural species, the douglas squirrel and red squirrel. I hypothesize that the two urban species will have a higher degree of behavioral flexibility and a lower degree of sensitivity to human disturbance than the two rural species. If urban species have greater behavioral flexibility, I would predict that they will be less neophobic (fear of novel objects) and be more successful at exploiting novel objects through problem solving than rural species. Observational (social) learning has been shown to be a more efficient method of acquiring the ability to exploit novel resources than individual learning (Mason and Reidinger 1981). Thus, I would predict that urban species would have a greater ability to learn through observation than rural species. If urban species are less sensitive to

human disturbance, I would predict that they would have shorter flight initiation distances and have lower stress responses when captured and handled than rural species (Partecke et. al 2006).

If behavioral flexibility and tolerance to disturbance have enabled eastern grey squirrels and fox squirrels to colonize an urban environment, I would expect to see these traits in the rural native populations of these squirrel species. In other words, I hypothesize that these traits allowed these species to succeed by preadapting them to an urban environment (preadaptation hypothesis). If this hypothesis is supported, I would expect to see that native rural populations of urban species have a higher degree of behavioral flexibility and a lower degree of sensitivity to human disturbance than rural species.

Methods

A projected timeline of the methods is shown in Table 1.

Squirrel Collection and Maintenance

I plan to collect 20 individuals of each *T. hudsonicus* and *T. douglasii* in woodland areas where they occur in Washington. I also plan to collect 20 individuals of each *S. carolinesis* and *S. niger* in the suburban /urban areas where they occur. Preferably equal numbers of both males and females will be collected for each species. Subjects in captivity will be housed separately and be kept on a 23 hour food deprivation schedule during behavioral flexibility trials to ensure that they will be hungry before testing (Spies 1965).

Behavioral Tests

Behavioral flexibility

Each squirrel species will be tested in three correlates of behavioral flexibility: neophobia, problem solving, and social/observational learning.

Neophobia

Squirrels (n=20/ species) will be tested for neophobia by measuring their response to feed near a novel object based on the procedures by (Webster and Lefebvre 2001). For each trial a squirrel will be presented randomly with either a food dish (control) or a food dish with a novel object placed near it in a separate cage. Latency to feed and time spent feeding will be recorded in a 20 minute period. Squirrels will be presented with three different novel objects in three separate trials. In addition, they will be presented with three control trials. The novel objects will include three straws of different colors sticking vertically out of a ball of paper, three springs, and a handful of curly white paper. Squirrels will be habituated to the food dish before trials begin, and I will conduct one trial per day for each squirrel. The difference in latency to feed and feeding times between the experimental and the control trial will be used to measure a species neophobia.

Problem Solving

To test each squirrel's ability to problem solve I will present each squirrel (n=20/ species) with a clear Plexiglas box filled with food (Webster and Lefebvre 2001; Fig. 1). The box can be opened and the food reached by lifting or pushing one of two lids each fitted with a metal ring and by pulling or pushing drawers also fitted with a metal ring. Before trials, squirrels will be habituated to the box by allowing them to eat from it with all the draws and lids open. For each 20 minute trial, I will record the latency to first contact the box and assess the squirrel's ability to problem solve by recording its success or failure to obtain food from the box and the number of times it attempted to open the box by pushing, pulling, or lifting one of the metal rings.

Social Learning

I will test for social/observational learning based on the procedures by Akins and Zentall (1996). Two individuals from each species will be trained on a apparatus where it must step on a

treadle which will give it access to food (Fig. 2). During the last few days of training (before testing), the demonstrators will be exposed to a "dummy" squirrel in the observer's chamber to ensure that the presence of an observer will not disrupt the demonstrator's performance. Each observer (n=18/ species) will be trained to feed from the feeder in the demonstrator's chamber and will be given 4-5 days of habituation in the observer's chamber with no demonstrator present. During the testing session, an observer will be exposed to a demonstrator of its own species for 10 minutes in a separate chamber where it can view the demonstrator (Fig. 2). Following the observation session, the demonstrator will be removed and the observer will be tested on the apparatus for 30 minutes. The latency for an observer to respond and the number of times the observer steps on the treadle will be recorded. Demonstrators will be used only once per a day.

Sensitivity to human disturbance

Flight initiation distance

Procedures to estimate flight initiation distance (FID) will be based on the methods of Blumstein (2003). To estimate FID, a resting or non-moving subject will be identified in the field and then approached at a steady pace of 0.5 m/s. The distance that the observer started walking toward a squirrel and the distance at which the focal squirrel moved away will be recorded. Distance will be measured in paces which will be converted to meters. To ensure that subjects are not measured twice, measurements will be taken in different locations. Subjects will be tested preferably in the summer when squirrels are active. FIDs for 20 individuals of each species will be measured.

Stress Response

To measure a squirrel's stress response to human disturbance, I will measure the squirrel's glucocorticoid levels after applying a standardized capture and handling stressor protocol, described by Wingfield et. al (1982), to the individual. These measurements will be taken on individuals in captivity (n=20/ species). A stress response is defined as the increase in corticosterone level over a 60 minute period. About 3 minutes after capturing, I will obtain a small sample of blood (50 μ L) from the squirrel. After collecting the initial sample, squirrels will remain in cloth bags for a 60-min period of restraint with subsequent blood samples taken at 5, 10, 30, and 60 min. Corticosterone will be measured by radioimmunoassay using the exact procedures described by Wingfield et. al (1982). To test for differences in the acute stress responses between urban and rural species, I will calculate the area under the curve of plasma corticosterone over time for each squirrel. Therefore I predict urban species will have smaller areas under these curves than rural species.

Preadaptation hypothesis

If I see a difference in behavioral flexibility and sensitivity to human disturbance between urban and rural species, I will collect 20 individuals each of *S. carolinesis* and *S. niger* in their native rural habitat in Illinois where they are both abundant (Rosenblatt et. al 1999) and measure their behavioral flexibility and sensitivity to human disturbance with the procedures described above. I will compare these measures to the rural and urban species.

Expected results and significance

Based on the results of Møller (2009) and Timmermans and Lefebvre (2001), I would expect to see a difference in behavioral flexibility and sensitivity to human disturbance between urban and rural species. Urban environments are highly novel, and I would expect behavioral flexibility to be an important predictor in determining whether or not a species will succeed in an

urban environment. If not, then this suggests that there are other traits that explain why certain species squirrel are able to colonize urban environments over others. If there is a difference between urban and rural species, but the pre-adaptation hypothesis is not supported, this may suggest that urban species are able to readily acquire these traits when adapting to urban environments, which is an interesting find.

Comparing traits between urban and rural species is important because it allows us to understand why some species are able to persist in urban landscapes while other cannot. This will allow us to determine the most effective way to maintain high levels of biodiversity in human landscapes. For example, maintaining natural resources within the city will be important if native species do not have the behavioral flexibility to exploit novel resources.

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Table 1. Projected Timeline of Methods

Months	Experimental Task
June-September	Capture squirrels of each species
September-November	Neophobia Trials
November-December	Problem Solving Trials
December-March	Social Learning Trials
March-May	Stress Response Trials
June-September	FID measurements
September-October	Analyze results
February-April	Capture <i>S. carolinesis</i> and <i>S. niger</i> in Illinois
April-May	Neophobia Tests
May-July	Social Learning Tests
July-September	FID measurements

Months	Experimental Task
March-April	Stress Response Tests*
May-June	Analyze results

* All stress response measurements will be taken at the same time each year since season affects stress response levels (Partecke et. al 2006).

Animal Care and Ethics

- A) Does the proposed study involve endangered species or threatened populations? **NO**
- B) Does the proposed study involve trapping, netting, banding or in any other way potentially disturbing wild populations? **YES**
- C) Does the proposed research involve maintenance of animals in captivity? **YES**
- D) Will animals be subjected to pain? **NO**
- E) Will animals be killed? **NO**